Thermoregulatory traits combine with range shifts to alter the future of montane ant assemblages

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ABSTRACT

Predicting and understanding the biological response to future climate change is a pressing challenge for humanity. In the 21st century, many species will move into higher latitudes and higher elevations as the climate warms. In addition, the relative abundances of species within local assemblages is likely to change. Both effects have implications for how ecosystems function. Few biodiversity forecasts, however, take account of both shifting ranges and changing abundances. We provide a novel analysis predicting the potential changes to assemblage level relative abundances in the 21st century. We use an established relationship linking ant abundance and their colour and size traits to temperature and UV-B to predict future abundance changes. We also predict future temperature driven range shifts and use these to alter the available species pool for our trait-mediated abundance predictions. We do this across three continents under a low greenhouse gas emissions scenario (RCP2.6) and a business-as-usual scenario (RCP8.5). Under RCP2.6, predicted changes to ant assemblages by 2100 are moderate. On average, species richness will increase by 26%, while species composition and relative abundance structure will be 26% and 30% different, respectively, compared with modern assemblages. Under RCP8.5, however, highland assemblages face almost a tripling of species richness and compositional and relative abundance changes of 66% and 77%. Critically, we predict that future assemblages could be reorganised in terms of which species are common and which are rare: future highland assemblages will not simply comprise upslope shifts of modern lowland assemblages. These forecasts reveal the potential for radical change to montane ant assemblages by the end of the 21st century if temperature increases continue. Our results highlight the importance of incorporating trait-environment relationships into future biodiversity predictions. Looking forward, the major challenge is to understand how ecosystem processes will respond to compositional and relative abundance changes.

INTRODUCTION

Climate change has significant implications for human prosperity and the biodiversity on which it depends (IPCC, 2014; Pecl *et al.*, 2017). As a result, generating predictions of the state of biodiversity following climate change is now a major goal for ecologists and environmental scientists (Urban, 2015). The most frequently reported and predicted changes are large-scale species range shifts. As the climate warms, species move to remain within their environmental niche. This leads to dramatic shifts of species away from the equator and the lowlands, and into high latitude and high elevation areas as global temperature regimes change (Parmesan & Yohe, 2003; Parmesan, 2006; Chen *et al.*, 2011; Poloczanska *et al.*, 2013; Warren & Chick, 2013). These range shifts can result in increased extinction risk for individual species (Erasmus *et al.*, 2002; Visser & Both, 2005; Urban, 2015; Pecl *et al.*, 2017) and could have large consequences for ecosystem functioning and stability as assemblages of species are reorganised (Walther, 2010).

Changes to species distributions, however, are only one manifestation of a suite of ecological changes that are expected to result from 21st century climate change. These include alterations to demography, and to the absolute and relative abundances of individuals within their geographic ranges (Johnston *et al.*, 2013; Crase *et al.*, 2015; Gaüzère *et al.*, 2015; Tayleur *et al.*, 2016; Bowler *et al.*, 2017). Understanding and predicting this small-scale assemblage level response to climate change has been repeatedly highlighted as a key, but often neglected, component of our ecological forecasting toolbox (Suding *et al.*, 2008; Walther, 2010; Urban *et al.*, 2016). This matters because an assemblage where a single species makes up 90% of the individuals, for example, and an assemblage where all species are represented equally will look and function very differently (Walther, 2010). Indeed, several studies of ecosystem functioning have shown how changes in the relative abundances or occurrences of one or more taxa can lead to large changes in the rates and modes of

function delivery (Slade *et al.*, 2007; Manning *et al.*, 2016; Griffiths *et al.*, 2018; Ashton *et al.*, 2019).

Despite the importance of both niche-based range shifts (i.e. species occurrence) and assemblage-level abundance changes in determining the future state of biodiversity following climate change, these two factors are rarely investigated in combination (but see Dullinger *et al.*, 2012). Many studies use species distribution modelling techniques to project future species ranges (Guisan & Thuiller, 2005; Colwell *et al.*, 2008; Urban *et al.*, 2016), and a growing literature is making use of species traits to predict how relative abundance changes may alter assemblages (Shipley *et al.*, 2006; Frenette-Dussault *et al.*, 2013; D'Amen *et al.*, 2015). Either large-scale range shifts or abundance-based assemblage changes could lead to species becoming extinct or newly dominant, but there is little explicit understanding of how they may interact with each other.

Previously, we found that darker coloured and larger bodied ant species dominate cold environments, such as high elevations and latitudes, while lighter coloured and smaller species tend to dominate in hotter environments (Bishop *et al.*, 2016; Gibb *et al.*, 2018). Darker colours typically enable organisms to heat up faster than if they had light colouration, while larger bodies lose heat more slowly than small bodies (Willmer & Unwin, 1981; Stevenson, 1985; Spicer *et al.*, 2017). This colour trend was reversed in hot environments with high UV-B levels - an effect that we hypothesized was influenced by the role of melanin in defending against harmful UV-B irradiation. The biophysical links between ambient temperature, UV-B, colour and body size that we suspect drive these patterns, however, are unlikely to be specific to ant assemblages. They operate at a range of scales and in a variety of taxa including dragonflies (Zeuss *et al.*, 2014; Pinkert *et al.*, 2017), butterflies (Ellers & Boggs, 2004), beetles (Schweiger & Beierkuhnlein, 2015), birds (Delhey, 2017), plants (Koski & Ashman, 2015) and microorganisms (Cordero *et al.*, 2018).

This trait-environment relationship is important because temperature will increase (IPCC, 2014), while the direction of change in UV-B irradiance will depend on geographic location and emission levels (Bais *et al.*, 2015; Lamy *et al.*, 2018) in the 21st century. Critically, these environmental changes will act through species traits to favour some species over others. Therefore, relative abundances at the local level will change in accordance with the body size and colouration of species. Several studies predict smaller body sizes (Sheridan & Bickford, 2011; Gibb *et al.*, 2018; Tseng *et al.*, 2018) and lighter (Zeuss *et al.*, 2014; Delhey, 2017) or darker (Roulin, 2014) colours for animals as the 21st century progresses.

Here, we combine predictions of potential trait-mediated abundance changes with anticipated range shifts to simulate how montane ant communities will respond to climate change. Ants are recognised as a major functional component of terrestrial ecosystems (Evans *et al.*, 2011; Zelikova *et al.*, 2011; Ewers *et al.*, 2015; Parr *et al.*, 2016; Griffiths *et al.*, 2018). Understanding how their diversity and assemblage structure is likely to change will be key to anticipating how entire ecosystems will be altered in the future. Furthermore, the continental scale of our dataset, and the observation of the trait-environment relationships in other taxa, makes for an important first step in understanding the potential impact of this relationship on future species abundances.

We forecast potential range shifts for our study species by using a simple climate-envelope model (Colwell *et al.*, 2008) based on projections of future climate and adiabatic lapse rates (the rate at which temperature declines with elevation). We forecast abundance changes by first predicting future assemblage averages of colour and body size and then using a maximum-entropy based model (Shipley *et al.*, 2006) to estimate the most likely distribution of species relative abundances. We simulate future changes under a reduced greenhouse gas emissions scenario (RCP2.6) and an unmitigated baseline scenario (RCP8.5) to provide an upper and lower estimate of possible biodiversity futures.

Specifically, we assess the potential for species richness and composition of montane ant assemblages to change throughout the 21st century if we base our predictions on trait-based abundance changes, range shifts or a combination of both. We also ask whether the combination of these two processes predicts the formation of non-analogous assemblages, i.e., assemblages for which there is no contemporary equivalent, in terms of species composition or relative abundance structure (Le Roux & McGeoch, 2008; Keith *et al.*, 2009).

METHODS

Observed data

We sampled epigaeic ant assemblages during the austral summer using pitfall traps on 14 elevational transects (108 separate elevational sites) across Africa, Australia and South America. Transects ranged from 0 to 3000 m a.s.l. (Bishop *et al.*, 2016). In Africa and Australia replicate pitfall trapping grids followed the same protocol. In South America, the spatial arrangement, number of traps and size of the traps differed slightly. All traps were placed during the austral summer and were open for 5 days and nights in Africa, and 7 days and nights in the Australia and South America. Further details on trapping materials are found in Appendix S1 and Bishop *et al.* (2016). For each transect, assemblages were pooled at the elevational band level (bands were separated from each other by 100 to 300 vertical metres) for this analysis. For each species, we recorded body size, as measured by Weber's length. Weber's length is defined as the length between the anterodorsal margin of the pronotum and the posterodorsal margin of the propodeum and is a commonly used measure of body size in ants (Brown, 1953). We recorded Weber's length to the nearest 0.01 mm. We recorded colour as a categorical variable using a predetermined set of colours by a limited number of observers. We converted these colours to HSV (hue, saturation and value) values

and retained the v (value, or lightness) as a measure of how light or dark in colour a species is. This measure of lightness is bounded by 0 and 1. Values of 0 are dark while values of 1 are light. Both traits were recorded from six specimens per species per elevational transect, where possible. Further details can be found in Bishop *et al.* (2016) and in Appendix S1.

We calculated assemblage weighted means (AWM) of body size and colour lightness for the ant assemblages using the formula:

$$AWM = \sum_{i=1}^{S} p_i x_i$$

Where S is the number of species in an assemblage, p_i is the proportional abundance of each species and x_i is the trait value (lightness or body size) of each species. The difference between this analysis and that in Bishop *et al.* (2016) is that here, replicate assemblages within the same elevational band on the same elevational transect are pooled together to form a single assemblage.

We assessed the relationship between each assemblage-weighted trait (colour lightness and body size) and temperature and UV-B irradiance using linear mixed models (LMMs). Current temperature and UV-B data were taken from the climatic surfaces WorldClim 2 (Fick & Hijmans, 2017) and glUV (Beckmann *et al.*, 2014), respectively. We extracted mean temperature and UV-B irradiation for January to March (the austral summer months, when we sampled ants) for each elevational transect and took an average within each elevational band. As temperature and UV-B are correlated, we used the residuals of the relationship as the UV-B variable. We used second order polynomial terms to detect curvature and an interaction between temperature and residual UV-B was included. Assemblage weighted lightness was logit-transformed prior to modelling with a Gaussian distribution. To account for the geographical configuration of our study sites we used a nested random effects

structure of transect within mountain range within continent. We centred and scaled all explanatory variables. We used bias corrected Akaike information criterion (AICc) values to compare all possible models. Each of the 108 data points used in these models represents an assemblage of ants from a single elevational band.

We tested our dataset for structural bias in the AWMs by randomly shuffling the traits of each species within a given regional pool and refitting the mixed effects models 2000 times (Hawkins *et al.*, 2017). We used the same explanatory variables as selected by the best fitting original models and extracted a marginal R^2 (R^2_m = due to fixed effects only) for both colour and body size for each randomisation. We compared our original R^2_ms to the randomly generated R^2_ms. For colour and body size, our original R^2_ms were in the 1^{st} and 0.99^{th} percentile, respectively (Appendix S2). This means that randomly assigning species names to trait values could not recreate our observed patterns – implying that there is no problem of structural bias in this dataset influencing the trait-environment relationship (Hawkins *et al.*, 2017).

Future data

We use two different climate change scenarios to make future projections of montane ant biodiversity. We use Representative Concentration Pathway (RCP) 2.6 and RCP8.5. RCP2.6 predicts a mean increase in temperature, relative to preindustrial levels of 1°C (range of 0.3-1.7°C) by 2100 while RCP8.5 predicts an increase of 3.7°C (range of 2.6-4.8°C IPCC, 2014). If greenhouse gas emissions are in line with the Paris Agreement of 2015, then RCP2.6 is a likely future climate scenario. If not, and emissions continue on their current trajectory, the planet faces the future that RCP8.5 describes (Sanford *et al.*, 2014). We extracted estimates for regional temperature change from the IPCC (2014) for all of our study sites for RCP2.6 and RCP8.5. UV-B irradiance will also change in the 21^{st} century. We use

predicted estimates of UV-B change under RCP2.6 and RCP8.5 for all of our study sites from Lamy *et al.* (2018). As both the IPCC (2014) temperature data and Lamy *et al.* (2018) UV-B irradiance data are given in relative or percentage change, we calculate absolute values for the 21st century based on our observed data from the WorldClim 2 and glUV surfaces.

We generated predictions of future assemblage weighted colour lightness and body size for all sites by combing the observed LMMs of colour and body size with the time series of future temperature and UV-B changes. We used the "predict.lme" function in R (Bates *et al.*, 2014) to predict future AWM colour lightness and body size under future temperature and UV-B conditions. As a result, predictions of future AWM lightness and body size were driven by changing temperatures and changing UV-B irradiation levels. Predictions of future AWMs were made for each year from 2011-2100.

Trait simulation

In the trait simulation, we forecast the state of future ant assemblages based only on changes to relative abundance predicted by the trait-environment relationship. We did not simulate dispersal: species were not permitted to move out of the sites in which we originally observed them. We use a Community Assembly by Trait-based Selection (CATS) model (Shipley *et al.*, 2006; Shipley, 2010; Sonnier *et al.*, 2010). The CATS model predicts the relative abundances of different species given a defined species pool, the traits of those species and the expected average trait value (assemblage weighted mean, AWMs) (Shipley *et al.*, 2006; Laughlin & Laughlin, 2013).

The CATS model uses a series of constraint equations to produce a set of possible vectors of species relative abundances (Shipley, 2010; Laughlin & Laughlin, 2013). First, the model constrains abundances to sum to 1:

197 $$\sum_{i=1}^{S} p_i = 1$$

198 Where p_i is the predicted abundance of species i and S is the number of species in the pool.
199 This constraint equation is always the same.

200 Second, the model constrains the set of possible relative abundance vectors depending on the
201 predicted AWM:

202 $$\sum_{i=1}^{S} t_i p_i = \bar{T}$$

203 Where p_i is the predicted abundance of species i, t_i is the trait value of species i, S is the
204 number of species in the pool and $\bar{T}$ is the AWM. This constraint equation differs across
205 different sites (and in our case, through time) as the supplied AWM ($\bar{T}$) changes. This
206 equation refines the set of possible relative abundance vectors to those that produce the same
207 AWM as that supplied.

208 The final prediction is made using only one vector from the set. The final vector is that which
209 maximizes the relative entropy function:

210 $$H(p, q) = -\sum_{i=1}^{S} p_i \ln(p_i/q_i)$$

211 Where ln is the natural log, p_i is the predicted abundance of species i, q_i is the prior
212 probability of species i and S is the number of species in the pool. The solution with the
213 highest entropy is that which minimises the difference between the predicted abundances (p_i)
214 and the prior information (q_i). Under a maximally uninformative prior, where all species have
215 the same probability of selection, the model will choose the most even distribution of species
216 abundances. Under all other cases, the function will choose the vector which deviates the

217 least from the prior information. Further information on the mathematical formulation of the
218 CATS model and it's comparison to other trait-based predictive frameworks can be found in
219 Shipley (2010), Shipley *et al.* (2006) and Laughlin and Laughlin (2013). We use this CATS
220 approach to predict relative abundances of mountain-top ants into the 21st century (further
221 information in Appendix S3).

222 Before running the simulation, we tested how well CATS could predict the observed relative
223 abundances of ants in all of our assemblages when provided with prior information on which
224 species were present in each elevational band. We calculated R^2 to measure how well the
225 predicted relative abundances matched the observed. The CATS model was implemented
226 using the "maxent" function in the "FD" package of R (Laliberté & Shipley, 2011).

227 We ran the CATS model for each elevational band, from each elevational transect, from the
228 observed data year (arbitrarily assigned as 2010) to 2100. In each year, we supplied our
229 predictions of future AWM colour lightness and body size. We assigned species not present
230 in a given elevational band a prior of 0 and those that were present an even probability of
231 selection. This prior means that species richness cannot increase under this simulation. The
232 output from this procedure was a vector of relative abundances for each year of the
233 simulation, for each elevational band, within each mountain transect and for each RCP
234 scenario.

235 If a species' predicted relative abundance was less than 0.0001 (one in ten thousand), it was
236 classed as extinct and was removed from the available species pool. Consequently,
237 assemblages in this simulation could lose species but they could not gain them. This
238 threshold of relative abundance was based on the smallest relative abundance recorded from
239 our field observations. Different thresholds around this value make little difference to our
240 results (Appendix S4).

241

242 **Range Shift Simulation**

243 In the range shift simulation, we forecast the future state of ant assemblages using a simple
244 climate-envelope model. As a result, this simulation predicted future species occurrence only,
245 not relative abundance. There are limited data available on the geographic ranges of the
246 species in our study beyond this dataset itself. As a result, we are unable to incorporate the
247 entire geographical ranges of these species into comprehensive species distribution models.
248 We use the simple method developed by Colwell *et al.* (2008) to assess potential elevational
249 range shifts using only temperature for transect data. Consequently, we interpret our forecasts
250 as potential changes in elevational range.

251 We first calculated the elevational distributions for all species in the dataset. We set the
252 distribution of each species to encompass the highest and lowest elevations from which we
253 sampled it. We assume ranges are inclusive and recorded a species as being present at all
254 elevations between the highest and lowest recorded occurrences. We set range limits to
255 extend halfway to the next neighbouring elevational band above and below (Colwell *et al.*,
256 2008). Second, we calculated empirical adiabatic lapse rates, the rate at which temperature
257 declines with elevation, for each mountain. We estimated the slope of the relationship
258 between temperature and elevation for each mountain using simple linear regression and used
259 this as the adiabatic lapse rate. We simultaneously used WorldClim 2 and data logger
260 estimates of temperature. For the Australian transects and the Mariepskop transect in South
261 Africa we only used WorldClim 2 estimates. Table S5 shows the estimated lapse rates for
262 each transect.

263 We used the data on species elevational distributions, adiabatic lapse rates and predicted
264 future temperature changes to predict the shifting ranges of the ant species on each transect
265 and, by extension, the shifting assemblage compositions, into the 21st century. Ranges were

shifted upslope relative to the observed baseline depending on the predicted temperature increase or decrease for a given year. The rate of this vertical movement was set by the adiabatic lapse rate of each transect. This procedure is identical to that used by Colwell *et al.* (2008). All species on the same transect move upslope at the same rate. Across the entire dataset, the average upslope shift by 2100 was 145 m for RCP2.6 and 1050 m for RCP8.5. When a species range overlapped with a sampling site at a given time point, it was classed as present.

Combined Simulation

The final simulation combines the trait and range shift simulations. The combined simulation runs in almost the same way as the trait simulation. We predict relative abundance changes based on predicted changes in AWM lightness and body size using CATS. Behind this process, however, is a changing species pool. Whereas the trait simulation was static and did not allow new species to enter a given elevational band, the combined simulation moves species upslope (and downslope) through time according to their predicted range changes. As a result, the available species pool that the CATS model is able to select from changes as the simulation runs. We ran this simulation under RCP2.6 and RCP8.5.

Interpretation

It is not possible to predict accurately patterns of change all the way to 2100 for some lowland assemblages under the range shift and combined simulations because we do not have data on the species that may enter these areas from even lower elevations or lower latitudes. This could cause an artificial lowland biotic attrition in these locations (Colwell *et al.*, 2008). For each year we use the predicted temperature change and the adiabatic lapse rate of each

mountain to calculate where the "lower predictive limit" is. We only include data from assemblages that are above this limit in a given year (Appendix S6). This means that we exclude the very lowest assemblages on each mountain, and that there are fewer predictions available in 2100 compared with earlier years. This effect is less severe in RCP2.6 than RCP8.5 due to the smaller temperature change.

For each simulation and climate change scenario, we extract five different metrics from each year in the 21st century and plot these through time. These metrics are: (1) percentage change in species richness, (2) percentage of the original fauna lost, (3) Sørensen's total compositional dissimilarity, (4) Simpson's turnover-based dissimilarity and (5) the abundance weighted Bray-Curtis dissimilarity. All measures are relative to the start of the simulation. For example, we calculate dissimilarities as the dissimilarity between a given year and the year 2010 (our observed data), while the species richness metrics are all proportional to the richness values recorded in 2010. We calculate the average and 95% CI across sites for each of these metrics through time separately for RCP2.6 and RCP8.5. For the range shift and combined simulations, the year 2010 is based on our current predictions, rather than current observations. Our current predictions have slightly elevated species richness (11 ± 0.03 % , mean ± SE) due to the interpolation of species ranges. We compared current predictions to future predictions to avoid artificially inflating the degree of change estimated due to our range interpolation procedure alone.

To detect the formation of non-analogous assemblages in the combined simulation we find the closest modern (year 2010) assemblage, from any elevation, in terms of species composition for each future (year 2100) assemblage. We use Sørensen's dissimilarity metric to do this. We then calculate the abundance-based dissimilarity between the future assemblages and their closest modern analogue using Bray-Curtis similarity. Large Sørensen's dissimilarities would indicate that future assemblages have no modern analogue,

as this is an occurrence-based metric. Alternatively, a low Sørensen's dissimilarity but a high Bray-Curtis dissimilarity would indicate that future assemblages have similar species compositions to modern assemblages, but different distributions of relative abundance. Between these pairs of future assemblages and their modern analogues, we also calculate a mean and maximum rank shift, expressed as a percentage of the largest possible shift. To do this we calculate the rank abundance of each species in each of the future-modern analogue pairs. We then calculate the absolute change in ranks between each species and divide either the maximum change or the mean change by the number of species. This is an extension of the mean rank shift metric of Collins *et al.* (2008).

RESULTS

As expected, we recovered the same trait-environment relationship as in Bishop *et al.* (2016) after pooling at the elevational band level within a transect - ant assemblages were, on average, darker in colour and larger in worker body size in cold environments (Fig. S7). The CATS model performed well and predicted 75% of the variation in observed relative abundances. This level of accuracy is comparable with previous studies, for example, Frenette-Dussault *et al.* (2013) reported an accuracy of 40% when using two traits and ~70% when using six traits. We use only two traits here.

Occurrence metrics

Predicted species richness changes varied strongly by simulation type and climate change scenario (Fig. 1). Across all three simulations, assemblages showed larger changes to overall richness and lost more of their original fauna in RCP8.5 compared with RCP2.6. In the trait

simulation, species richness declined by 10% in RCP2.6 and by 15% in RCP8.5, averaged across all assemblages by 2100 (Fig. 1a, d). In the range shift simulation, species richness increased by 29% in RCP2.6 and by 193% in RCP8.5, averaged across all assemblages by 2100 (Fig. 1b, e). In addition, 14% of the original fauna was lost in RCP2.6 and 43% in RCP8.5. In the combined simulation, the change in species richness was not as much as in the niche simulation (RCP2.6 = 26%, RCP8.5 = 186%, Fig. 1c) but a larger fraction of the original fauna was lost (RCP2.6 = 20%, RCP8.5 = 47%, Fig. 1f).

Predicted compositional changes also varied strongly by simulation type and climate change scenario (Fig. 2). Again, predicted changes were much greater under RCP8.5 compared with RCP2.6. In the trait simulation, compositional dissimilarity (as measured by Sørensen's dissimilarity) by 2100 was 0.07 in RCP2.6 and 0.11 in RCP8.5, on average (Fig. 2a). This was entirely due to nested patterns of compositional change as the trait simulation only allows for extinction, not colonisation (as measured by Simpson's dissimilarity, Fig. 2d). In the range shift simulation, compositional dissimilarity by 2100 was 0.22 under RCP2.6 and 0.64 under RCP8.5 (Fig 2b). In RCP2.6 this overall compositional dissimilarity was almost evenly made up of turnover and nestedness (average turnover by 2100 for RCP2.6 = 0.1, Fig. 2e). For RCP8.5, turnover was a larger component of overall compositional dissimilarity (average turnover by 2100 for RCP8.5 = 0.41, Fig. 2e). In the combined simulation, a similar pattern to the niche simulation was seen for both total compositional dissimilarity (RCP2.6 = 0.27, RCP8.5 = 0.65, Fig. 2c) and turnover dissimilarity (RCP2.6 = 0.12, RCP8.5 = 0.38, Fig. 2f).

359

360 *Abundance metrics*

361 Predicted abundance weighted dissimilarity is greater for RCP8.5 than for RCP2.6 and shows
362 differences between the trait and combined simulations (Fig. 3). In the trait simulation,
363 abundance dissimilarity is 0.15 by 2100 under RCP2.6 and 0.37 under RCP8.5 (Fig. 3a). In
364 the combined simulation, abundance dissimilarity is 0.33 by 2100 under RCP2.6 and 0.78
365 under RCP8.5 (Fig. 3b).

366

367 *Modern-future analogues*

368 While future assemblages tended to have a close modern analogue in terms of species
369 occurrence, this was not true when considering assemblage structure and relative abundances.
370 The average occurrence-weighted Sørensen's dissimilarity between predicted assemblages in
371 2100 and their closest modern analogue was 0.08 for RCP2.6 and 0.11 for RCP8.5 (Fig. 4a).
372 The average abundance-weighted Bray-Curtis dissimilarity between these same pairs of
373 future and modern assemblages was 0.36 under RCP2.6 and 0.51 for RCP8.5 (Fig. 4a). In
374 RCP2.6, average mean rank shift was 19% and average maximum rank shifts were 42%. For
375 RCP8.5, the average mean rank shift was 30% and the average maximum was 70%. A
376 maximum rank shift of 100% is the highest possible, whereby the most common species
377 becomes the rarest species, or vice versa.

DISCUSSION

We have forecast the future of mountain ant diversity using a novel combination of trait-mediated abundance predictions and temperature driven range shifts. We find that ant assemblages are likely to change drastically in terms of species richness, composition and abundance structure by 2100. In addition, we predict that while future assemblages will have modern analogues in terms of species occurrence, they will have an entirely different abundance distribution. These changes are likely to have a significant impact on the way these mountain systems function as ants mediate ecosystem processes and interact with many other members of the food web (Gómez & Oliveras, 2003; Zelikova *et al.*, 2011; Parr *et al.*, 2016). Our findings differ strongly, however, between alternative scenarios of climate change. Our predictions of species richness changes are much more optimistic under RCP2.6, which is a likely climate future only if the greenhouse gas emissions targets set at the Paris Climate Agreement of 2015 are met (Sanford *et al.*, 2014).

Biodiversity forecasts are expanding beyond shifting distributions (Pearson & Dawson, 2003) to predict assemblage level information, phylogenetic and functional diversity (Del Toro *et al.*, 2015; Graham *et al.*, 2017), and to incorporate a variety of biotic effects such as species interactions (Araújo & Luoto, 2007) and dispersal abilities (Dullinger *et al.*, 2012). Here, we provide a novel analysis predicting assemblage level relative abundances and potential range shifts from an established trait-environment relationship. The general form of the trait-environment relationship we use here appears to be a feature of many ectotherm assemblages and populations (Zeuss *et al.*, 2014; Pinkert *et al.*, 2017). The data we use are also relatively more straightforward to collect compared with species interaction coefficients or dispersal abilities, and simpler to assess for completeness compared with data for interaction networks (Vizentin-Bugoni *et al.*, 2016). Directional changes to species relative abundances may also

be easier to detect through time compared to species occurrences, because changes in species' rank abundances are more sensitive to change than occurrences, highlighting the usefulness of long-term monitoring schemes. As a consequence, the approach is a useful additional one for assessing assemblage level changes, which have been highlighted as a key requirement for the ecological forecasting toolbox (Suding *et al.*, 2008; Walther, 2010; Urban *et al.*, 2016).

Central to our forecasts are the different kinds of assemblage level change that each simulation emphasises. Both the trait and range shift simulations are unrealistic in isolation, but provide a minimum estimate of each effect in the absence of the other. The combined simulation predicts a unique set of future assemblages that neither the trait nor the range shift simulation could predict on their own. Under the combined simulation, we predict that future assemblages will support a similar set of species to modern ones from further downslope (similar observations have been made for plants and moths, Vittoz *et al.*, 2008; Chen *et al.*, 2009), but that their abundance structure will be reorganised (Fig. 4). This means that assemblages will not simply move upslope unchanged as the climate warms – they will also face a reorganisation in terms of which species are common and which are rare.

Notably, most work on the formation of non-analogous assemblages focuses on novel species co-occurrences (Keith *et al.*, 2009; Graham *et al.*, 2017). Our forecasts, however, show that changes to abundance may be an underappreciated aspect of non-analogous assemblage formation and highlight the importance of considering both species occurrence and relative abundance (Walther, 2010; Simpson *et al.*, 2011). The way in which these changes play out in reality, however, will depend on the form of the dispersal kernels across the species in the assemblages involved (Urban *et al.*, 2012; Alexander *et al.*, 2017) and the reorganisation of biotic interactions. At this stage, however, there are no independent data (Early & Keith,

2019) to assess inter- and intraspecific interactions among ants at these scales and inferring this information is fraught with difficulty (Stuble *et al.*, 2017)

All the changes we predict are likely to have a significant impact on ecosystem functioning and energy flow in mountain environments, especially given the numerical and functional dominance of ants in many terrestrial ecosystems (Griffiths *et al.*, 2018). We predict that future high elevation assemblages will likely contain more species than they do now. Given the positive relationship between ant diversity and the rate of ecosystem functioning (Fayle *et al.*, 2011; Griffiths *et al.*, 2018) it may be that, as more species move upslope, ant mediated functions such as scavenging, waste removal and seed dispersal will increase. This picture is complicated, however, by our prediction of large changes to the relative abundances of species based on their traits. By 2100, the assemblage weighted mean body size in our dataset will be 11.5% smaller under RCP8.5, on average, which suggests that the species responsible for performing ecosystem functions will also be smaller – the consequences of this for functioning are hard to predict. While we are certain that the role of ants in mountain ecosystems will change substantially in the future, we can only speculate on the ways in which this will happen.

Although our forecast for the future under RCP8.5 predicts large changes to ant biodiversity in mountain regions, our predictions under RCP2.6 are much more optimistic. Under this scenario of climate change, we expect species ranges to move upslope by 145 m and, correspondingly, our estimates of species loss, species gain and compositional and abundance change are much reduced in comparison to RCP8.5. What seems to be shared between the two scenarios, however, is the formation of abundance-based non-analogue assemblages. In RCP2.6, the degree of rank abundance reorganisation is smaller in comparison to RCP8.5, but remains substantial (Fig. 4). In sum, we support the view that reducing greenhouse gas

emissions and limiting temperature rises to below 2°C by 2100 is necessary for positive outcomes for global conservation and ecosystem integrity (Warren *et al.*, 2018).

Our simulations of range shifts assume a "full dispersal scenario" (Colwell *et al.*, 2008; Fitzpatrick *et al.*, 2011). Species ranges move upslope as the climate warms and there are no lags or limits in dispersal capacity. This is probably a reasonable assumption to make for ants. The geographic distances between different elevations in our dataset are relatively small, ants are renowned dispersers (e.g. Wilson, 1961) and winged reproductive individuals may be aided by updrafts in montane environments. On the other hand, it has been argued that the social and modular nature of ant colonies confers a high degree of persistence in the face of environmental perturbations and extremes (Andersen, 2008). This kind of non-equilibrial process may limit the available space for newly arrived dispersers to establish. This establishment limitation is especially true when considering competitive interactions between dominant and subdominant ant species, the outcome of which can also be influenced by temperature (Parr, 2008; Roeder *et al.*, 2018). These effects would disrupt the "full dispersal scenario" that we have assumed. Determining in more detail which factors limit or promote species distributions, dispersal ability and establishment capacities will greatly increase our ability to predict and understand future change (Fitzpatrick *et al.*, 2011; Alexander *et al.*, 2017).

In addition to processes such as competition and establishment limitation disrupting our simulation assumptions, vegetation-mediated changes to microclimate and soil properties may have a large influence on ant assemblages in the 21st century (Ríos-Casanova *et al.*, 2006; Munyai & Foord, 2012). The real world is more complicated than we can currently simulate and, because of this, we interpret our results as reflecting the maximum potential of range shifts and thermoregulatory traits to influence assemblage-level change.

In particular, our range shift simulation is relatively simple. Due to the lack of information available on full species ranges, dispersal abilities and biotic interactions, we were restricted in the modelling tools available that could predict elevational range shifts. Consequently, we used the method developed by Colwell *et al.* (2008) to minimise the assumptions we made about the biology and ecology of the ant species involved. The caveats are that our data may be underestimating true species ranges; that microclimatic variation removes the necessity for species to migrate upslope; and that the influence of biotic interactions between newly dominant or co-occurring species are ignored. Collecting the necessary data to account for these effects is an ongoing challenge (Early & Keith, 2019), particular for invertebrates.

In summary, we predict large changes to mountain ant assemblages due to temperature driven range shifts and trait-mediated abundance change. Many more species will be present in high elevation sites in the future, as has been found for plants (Steinbauer *et al.*, 2018), and their composition and abundance structure will change substantially. These changes will be much larger under RCP8.5 than RCP2.6, but both scenarios predict a future where highland assemblages are compositionally analogous to lowland ones but with a reorganised abundance structure. Going forward, it will be critical to understand how changes in relative abundance will contribute to cascading effects on the wider food web and ecosystem functioning.

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TABLES

No tables.

FIGURE CAPTIONS

Figure 1. *Plots showing predicted changes in species richness (expressed as a percentage change, a-c) and the original fauna (expressed as a percentage of the original fauna lost, d-f) for trait, range shift and combined simulations. Blue lines refer to predictions made for RCP2.6, red lines are for RCP8.5. Lines are loess smoothed averages taken from across all assemblages and mountain transects. Coloured polygons represent 95% confidence intervals.*

Figure 2. *Plots showing predicted changes in total compositional dissimilarity (Sørensen's dissimilarity, a-c) and turnover dissimilarity (Simpson's dissimilarity, d-f) for trait, range shift and combined simulations. Blue lines refer to predictions made for RCP2.6, red lines are for RCP8.5. Lines are loess smoothed averages taken from across all assemblages and mountain transects. Coloured polygons represent 95% confidence intervals.*

Figure 3. *Plots showing predicted changes in abundance weighted dissimilarity (Bray-Curtis) for trait and combined simulations. Blue lines refer to predictions made for RCP2.6, red lines are for RCP8.5. Lines are loess smoothed averages taken from across all assemblages and mountain transects. Coloured polygons represent 95% confidence intervals. No plot is presented for the niche simulation because it uses only occurrence data.*

Figure 4. *Plots showing the relationship between future assemblages in the combined simulation and their closest modern analogues. In (a), dissimilarity between future assemblages and their closest modern analogues is given. Modern analogues are those with*

749 *the smallest occurrence-weighted dissimilarity ("Occ.", Sørensen's dissimilarity).*
750 *Abundance-weighted dissimilarity ("Abund.", Bray-Curtis) between the future and closest*
751 *modern analogues is also given. Panels (b) and (c) show the average and maximum change*
752 *in rank abundance between future and modern pairs, expressed as a percentage of the largest*
753 *possible shift in rank. Blue boxes are for RCP2.6, red boxes are for RCP8.5.*